

FORAGING SPEEDS OF WARBLERS IN LARGE POPULATIONS AND IN ISOLATION

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Earlier, I (Morse 1968) demonstrated that during the middle of the breeding season female spruce-woods warblers (*Dendroica* spp.) foraged significantly faster than did their mates, a pattern subsequently reported in a number of other warblers (e.g., Black 1975, Sherry 1979). I attributed this difference to the females performing all of the incubation and a majority of the feeding of newly-hatched young, thus putting their foraging time at a premium. Data subsequently gathered on nearby island isolates of the same populations of 2 species (Morse 1971, 1977), combined with data on standing crops of insects in both mainland and island forests (Morse 1976a, 1977), make it possible to assess foraging speeds of Black-throated Green (*Dendroica virens*) and Yellow-rumped (*D. coronata*) warblers further.

Data on insect standing crops provide a common yardstick between the mainland and island populations. Their analysis suggests that no significant differences occur between the mainland and island areas except at the end of the season (Morse 1976a, 1977). Although standing crops may be imperfect indicators of productivity (e.g., Southwood 1966), insect faunas are similar on the islands and adjacent (shoreline) mainland plots (unpubl. data), and conditions influencing productivity (weather, etc.) are probably similar also. Therefore, the assumption of similarity in food availability seems reasonable. Given the limited foraging time available to all females and the high speeds at which mainland females forage at certain times, availability of insect food may be a critical factor at these times.

The islands studied differ from the mainland in that only 1 pair of any spruce-woods warbler species is present. Of 2 common nest predators on the mainland, the red squirrel (*Tamiasciurus hudsonicus*) is absent and the Blue Jay (*Cyanocitta cristata*) rarely visits. Both of these factors might lower the demands of nest attendance on females. Similarly, the absence of conspecifics might lower the demands for territorial proclamation and defense by the males. Male Black-throated Green Warblers sing considerably less on these islands than on the mainland (Morse 1970).

Given the apparent similarity in resource availability on the mainland and islands, the tendency for foraging speeds to fluctuate (Morse 1968), and the lessened demands on these individuals, one would predict island females involved with nesting activities to forage slower than mainland females. It is equivocal whether island males will forage slower than main-

land males when females are performing most of the nesting activities, since mainland males do not appear stressed in their foraging during this part of the cycle (Morse 1968). However, one would predict island males to forage substantially slower than mainland males when they are making major contributions to feeding fledged or nearly-fledged young.

STUDY AREAS AND METHODS

The "mainland" data were gathered on Hog Island (Todd Wildlife Sanctuary), Bremen, Lincoln Co., Maine. This is a large island of 132 ha covered by a mature red (*Picea rubens*) and white (*P. glauca*) spruce forest. It is separated from the mainland proper by a narrow channel, and its species composition is similar to that of the adjacent mainland (Morse 1976a). This forest is described in detail elsewhere (Morse 1968, 1976a, and references therein). The island data were gathered on 6 small nearby islands with spruce forests ranging from 0.35–1.50 ha. These islands are Crow and Jim's islands, Bremen, Lincoln Co.; Indian and Thief islands, Bristol, Lincoln Co.; and Ram and Crane islands, Friendship, Knox Co., Maine. They are described in detail elsewhere (Morse 1971).

Data on foraging speeds of island birds were gathered as described by Morse (1968). Briefly, in addition to data gathered on foraging sites (reported in Morse 1968, 1971), I scored birds for their rapidity of foraging movement. The scoring technique was adopted because individuals often became temporarily obscured in foliage so thick that detailed beak movements could not be observed, although rate of overall progress could nevertheless be ascertained accurately. This method was checked regularly on birds at sites where frequency of foraging could be observed closely. The following scores were used: 1 = 1–2 pecks/min, 2 = 3–4, 3 = 5–6, 4 = 7–9, 5 = 10–12, 6 = 13–15, 7 = 16–20, 8 = 21–25, 9 = 26–30, 10 = 31+.

The data on mainland foraging speeds were reported earlier (Morse 1968), and those from the islands were obtained during 1967–1969 while foraging data (Morse 1971) were being gathered. Analyses of insect standing crops were not available when the 2 foraging papers were prepared (Morse 1968, 1971), but were published later (Morse 1976a, 1977).

At least 12 pairs of each island and mainland group of warblers were studied, except island Black-throated Green Warblers, for which the sample consisted of 8 pairs. Each point in Fig. 1 represents observations at 10–200+ foraging sites.

Sampling of insects was carried out on the islands during the summers of 1968–1970, overlapping the period that foraging data were gathered. Insect sampling on the mainland was carried out during the summers of 1969–1972 and the mainland foraging data were gathered during the summers of 1966–1967. Since no noticeable insect outbreaks took place in the mainland forests during 1966–1967 and 1969–1972, and since rather similar arthropod biomasses occurred there during 1969–1972 (see Morse 1976a: Fig. 5a), I am proceeding under the assumption that the foraging of mainland birds was carried out under arthropod density regimes similar to those encountered during the summers of 1969–1972. Although I consider this to be a reasonable assumption, the reader should be aware of it, since insect outbreaks are not uncommon in forests and may have a marked effect on both the foraging patterns and abundance of insectivorous birds (e.g., Holmes and Sturges 1975, Morse 1978).

RESULTS

Foraging speeds of warblers are represented in Fig. 1, and significance levels between mainland and island individuals of the same species and

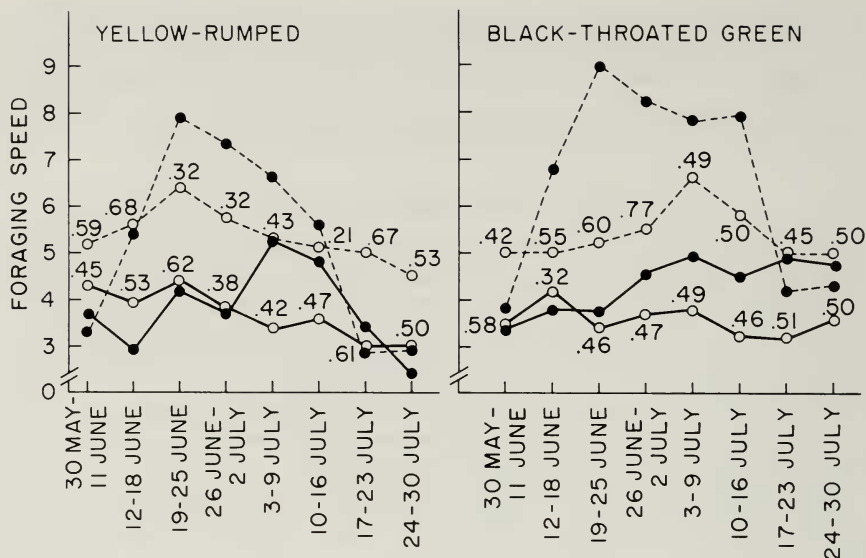


FIG. 1. Mean foraging speeds of male (solid line) and female (dashed line) warblers. Filled circles = mainland and open circles = islands. Mainland data points from Morse (1968). Standard deviations accompany each data point from an island. Standard deviations from mainland data points are published in Morse (1968, Fig. 5).

sex in Table 1. During the middle of the season, island females of both species foraged significantly more slowly than did mainland females. This period coincides with the time during which they incubate and feed young still in the nest (Palmer 1949; Morse 1968, unpubl. data). No significant differences in foraging speeds of females occurred immediately before this, the nest-building period, or at the end of the season, after young had left their nests. Island females of both species did, however, forage significantly faster at the very beginning of the season, which includes the period during which they search for nest-sites and accumulate resources for egg production. Only then did either island males or females forage significantly faster than their mainland counterparts (Table 1).

Island males of both species foraged significantly more slowly than mainland males during the middle of the season, a time coinciding with the first appearance of fledged young. This pattern held through the end of the season in Black-throated Green Warblers, but disappeared at the very end of the season in Yellow-rumped Warblers.

Island females always foraged faster than island males (Fig. 1), a difference that was statistically significant ($P < 0.05$ or less in 1-tailed Mann-Whitney U -tests) in all but 2 cases: 30 May–11 June for the Yellow-rumped

TABLE 1

LEVELS OF SIGNIFICANCE FOR DIFFERENCES IN FORAGING SPEEDS BETWEEN MAINLAND AND ISLAND WARBLERS^a

Date	Species and sex			
	Black-throated Green Warbler		Yellow-rumped Warbler	
	Male	Female	Male	Female
30 May–11 June	>0.05 (47, 217)	<0.001 ^b (43, 38)	>0.05 (25, 133)	<0.001 ^b (12, 69)
12–18 June	>0.05 (15, 132)	>0.05 (18, 35)	>0.05 (12, 192)	>0.05 (29, 72)
19–25 June	>0.05 (34, 43)	<0.001 (20, 12)	>0.05 (74, 92)	<0.001 (18, 33)
26 June–2 July	>0.05 (89, 61)	<0.001 (10, 21)	>0.05 (54, 105)	<0.001 (14, 52)
3–9 July	<0.01 (90, 49)	<0.05 (17, 75)	<0.05 (35, 115)	<0.001 (13, 56)
10–16 July	<0.001 (161, 12)	<0.001 (43, 16)	<0.05 (67, 108)	>0.05 (52, 34)
17–23 July	<0.025 (134, 18)	>0.05 (14, 14)	<0.025 (79, 77)	>0.05 (27, 16)
24–30 July	<0.05 (126, 10)	>0.05 (37, 17)	>0.05 (26, 29)	>0.05 (16, 13)

^a Number of observations in parentheses, with mainland birds preceding comma and island birds following comma.^b Island foraging speed faster than mainland foraging speed. In all other significant differences, mainland birds foraged faster than island birds; 1-tailed Mann-Whitney *U*-tests; *U*'s supplied by author upon request.

Warbler and 12–18 June for the Black-throated Green Warbler (Table 1). Both of these periods preceded the incubation stage of most individuals.

Foraging speeds of the 2 species shifted strikingly in concert over the season, greatly strengthening confidence in this analysis. In 7 of the 8 time periods island male Black-throated Green Warblers and island male Yellow-rumped Warblers simultaneously foraged significantly slower than did their mainland equivalents, or foraging speeds of these island and mainland birds were simultaneously not significantly different (Table 1) ($P = 0.035$, $N = 8$, in a 1-tailed binomial test). Results for females of the 2 species also corresponded in the same way during 7 of the 8 time periods ($P = 0.035$, $N = 8$), with the only difference being that in the first time period island females of both species foraged significantly faster than their mainland equivalents.

DISCUSSION

In that climatic factors and food availability were apparently similar on island and mainland study areas, most of these results may be attributed to differences in interference by other individuals and/or differences in danger of nest predation. Since no experiments were performed it is not possible to distinguish unequivocally between the alternatives, but strong inferences can be made.

Differences between island and mainland males can be tentatively attributed to levels of interference or potential interference, since the males make no contribution to incubation and little to new-born young (Morse

1968). Amounts of stationary singing by Black-throated Green Warblers were strikingly lower on islands during the middle of the season (Morse 1970) and, judging subjectively, a similar pattern seemed to hold for the Yellow-rumped Warbler as well. The stationary song of the Black-throated Green Warbler is given from prominent locations and seems associated with territorial display (Morse 1967, 1970). The slower foraging speed of the island males was thus probably a consequence of a modified time budget resulting from a decrease in frequency of stationary singing.

Differences in habitat use are unlikely to account for the differences in foraging speed of male Black-throated Green Warblers, since they used the same parts of both mainland and island vegetation (Morse 1971). Although island-dwelling Yellow-rumped Warblers did change their habitat use from that on the mainland (Morse 1971), the close parallels of their foraging speeds with those of the Black-throated Green Warblers mitigates against this shift being a major factor in the differences of their foraging speeds.

Differences in frequencies of interactions are unlikely to account for the differences in foraging speeds of mainland and island female warblers during the middle of the season, however. Even on the mainland only infrequent interactions were observed between females and other individuals (Morse 1976b) and mainland females' activities off the nest consisted almost entirely of extremely rapid foraging (Morse 1968).

The virtual absence of nest predators on these islands may be a more important factor affecting the foraging speed of females. Brood destruction is high where nest predators are common (Skutch 1976), and release from it could affect activity patterns strikingly. Unfortunately, I do not have comparative information on the attentiveness of females at island and mainland nests. However, attentiveness at mainland nests was extremely high, with these birds foraging for only short periods (Morse 1968). The greater ease that I experienced in observing island females (Morse 1971) suggests that they spent greater amounts of time off their nests than did mainland females. If correct, this interpretation means that attendance patterns of these warblers are only partially governed by thermoregulatory considerations and that the birds in question can adjust their attendance regimes in response to the presence or absence of nest predators about them. Current reviews of incubation behavior, oriented toward thermoregulatory aspects, make slight reference to pressures from nest predators as a possible modifier of attendance regimes at the nest (Ricklefs 1974, White and Kinney 1974).

I have no explanation for the greater foraging speeds of island females of both species at the very beginning of the season. Insect crops at that time were virtually identical, though variable, in the 2 areas (Morse 1977).

These were the only cases in which island birds foraged faster than their mainland counterparts.

SUMMARY

Male and female Black-throated Green and Yellow-rumped warblers isolated from conspecifics and nest predators on small islands foraged more slowly during the height of the breeding season than did ones in large mainland populations. Since food supplies on mainland and island were similar, differences between males are interpreted to result from a decrease in stationary singing associated with territorial maintenance, those between females a consequence of decreased nest attentive behavior associated with nest predators.

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